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STUDIES IN THE GENUS *CERATIUM* SCHRANK, WITH REFERENCE TO SPECIMENS COLLECTED IN THE AGULHAS CURRENT, IN PARTICULAR FROM A LINE OF STATIONS OFF PORT ELIZABETH, DURING INTERNATIONAL GEOPHYSICAL YEAR 1958: 1

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ABSTRACT

An historical review of the literature is given, followed by a taxonomic account of the Subgenus *Poroceratium* (Vanhöffen) Kofoid.

UITTREKSEL

STUDIES VAN DIE GENUS CERATIUM SCHRANK, MET VERWYSING NA MONSTERS WAT IN DIE AGULHASSEESTROOM VERSAMEL IS, VERAL VANAF 'N REEKS STASIES BUITE PORT ELIZABETH, GEDURENDE INTERNASIONALE GEOFISIESE JAAR 1958: 1.

'n Historiese oorsig van die literatuur word gegee asook taksonomiese verslag van die subgenus *Poroceratium* (Vanhöffen) Kofoid.

INTRODUCTION

Members of the genus *Ceratium*, are, with species of *Peridinium* Ehb., perhaps the most common of marine armoured dinoflagellates. Although many workers have studied *Ceratium*, the taxonomy is by no means completed, and cannot be, until cultural experiments determine the nature of variation; nor are many aspects of the biology fully understood.

The aim of the present account is to indicate the occurrence and degree of variation of the species in the Agulhas current, based on samples collected during I.G.Y. 1958. In these samples, routine investigations of the phytoplankton flora showed the armoured dinoflagellates to be much rarer than the diatoms. Accordingly, a more detailed examination was made of samples from the March and May cruises from the line of NGY stations off Port Elizabeth. (For data on the NGY stations see Zoutendyk 1960.)

Species of *Ceratium* in this area have been discussed or listed previously in general phytoplankton surveys: Karsten (1907), Taylor (1966), Nel (1968) and Thorrington-Smith (1969). A monograph of the genus from the Mozambique Channel has been published by Sournia (1967).

GENERAL FEATURES OF THE GENUS (See Fig. 1, A-F.)

The body is generally dorsiventrally compressed, and partly encircled by a transverse groove, the girdle, which divides it into an upper epitheca and a

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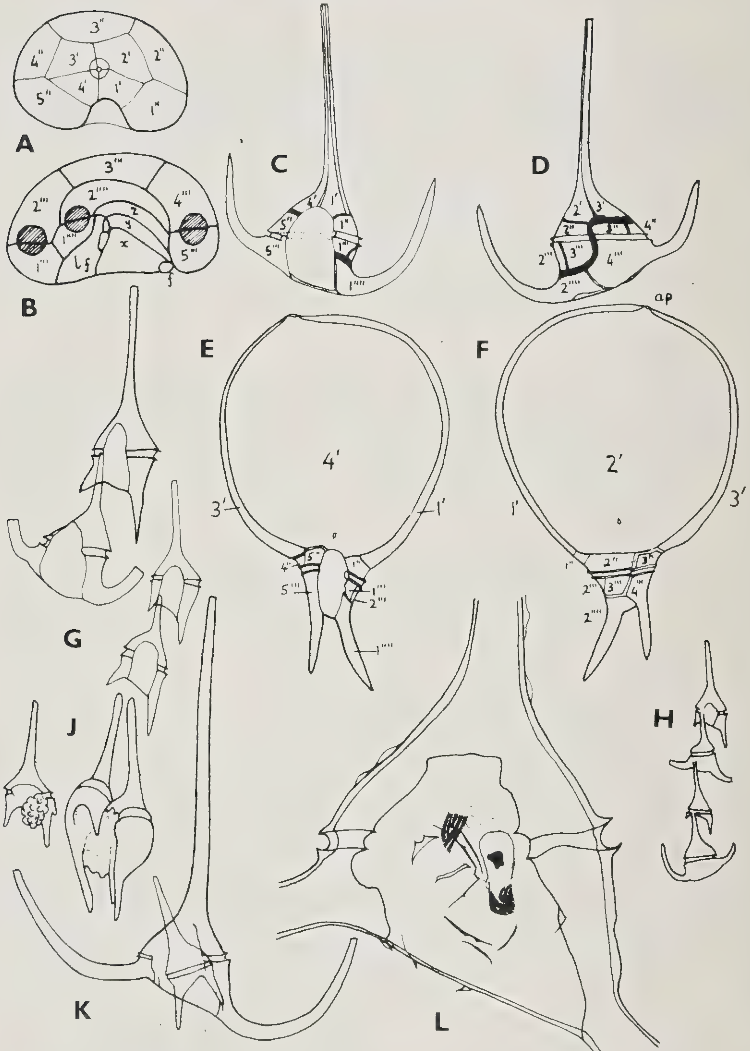
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Fig. 1.

lower hypotheca. The ends of the girdle lie ventrally on either side of the ventral area. The posterior margin of the body is oblique, the acute inclination in relation to the girdle being towards the right side of the body. On the left side of the ventral area is a longitudinal furrow or sulcus, containing the flagellar pore, from which the transverse flagellum encircles the body in the depression of the girdle, and the longitudinal flagellum is backwardly directed to some distance beyond the posterior margin of the cell.

The plate formula appears to be constant throughout the genus, being 4′, 0a, 5″, 5‴, 2⁗, that is, the epitheca is composed of four apical plates and five precingulars and the hypotheca of five postcingular and two antapical plates. The girdle is made up of four plates, the ventral area of three plates and the sulcus of two.

The epitheca is generally drawn out into an apical horn of varying length, composed of the anterior parts of the four apical plates. The apex of the epitheca or the tip of the apical horn possesses an apical pore. In all marine ceratia two antapical horns project from the hypotheca. The left antapical horn is formed from the two antapical plates, the right horn from part of postcingulars four and five. In the freshwater *C. hirundinella* (Müller) Bergh, the hypotheca may possess up to five antapical horns. All horns are hollow, surrounding extensions of the protoplast.

In schizogony, all the apical plates, precingulars one and two and postcingulars one to three, remain with the anterior daughter cell, while precingulars three to five, postcingulars four and five and both antapical plates are retained by the posterior daughter cell. Chains of cells arise due to adherence after schizogony. This tendency is more marked in some species than in others. The tip of the apical horn of the posterior cell rests ventrally on the right end of the girdle of the anterior cell. In the cells behind the front cell of a chain, the apical horn tends to be shorter, often markedly so.

Fig. 1. *A* and *B*, (Schiller 1937, original), showing plates of *C. hirundinella* (O.F.M.) Bergh: *A*, apical view, with apical horn and pore in centre; *B*, antapical view, with three antapical horns; 1′–4′ = apical plates, 1″–5″ = precingular plates, 1‴–5‴ = postcingular plates, 1⁗, 2⁗ = antapical plates, *x*, *y*, *z* = plates of ventral area, *lf* = sulcus, *f* = depression into which fits the apical horn of the posterior member of a chain; *C* and *D*, (Schiller 1937, after Jörgensen), showing plates of *C. tripos* (O.F.M.) Nitzsch: *C*, ventral view; *D*, dorsal view; the heavy line indicates division of plates during schizogony; *E* and *F*, (Kofoid 1907b), showing plates of *C. gravidum* Gourret: *E*, ventral view; *F*, dorsal view; *G*, (Lohmann 1908), "Temporalvariationen von *C. tripos balticum* . . . forma *lineata* . . . forma *truncata*", fragments of heteromorphic chains of *C. tripos; H*, the same, (after Tschirn 1920, fide von Stosch 1964); *J*, (after Entz 1924, fide Hall 1925), "coupling" in *C. hirundinella; K* and *L*, (von Stosch 1964), conjugation in *C. horridum* Gran: *K*, early stage; *L*, later stage, with fragments of thecal plates from the male gamete in the ventral area, the two nuclei lying adjacent to one another.

The epithecal plates are porulate and may be ornamented with a series of ridges in a linear to a reticulate pattern. The rims of the girdle are expanded into narrow membranous blade-like projections or lists and a list borders the left side of the sulcus. Lists, associated with the sutures between the relevant thecal plates, may occur at the base of the hypotheca, sometimes extending onto the adjacent part of the antapical horns, or on either side of the base of the apical horn, extending onto the epitheca; these lists, with smooth to serrated to denticulate margins, may be supported by spines. The thecal wall may be thickened along the sutures between plates, in particular along the sutures at the base of the hypotheca, and on one or both sides of the proximal parts of the apical and antapical horns.

AN HISTORICAL ACCOUNT OF THE LITERATURE DEALING WITH VARIOUS ASPECTS OF THE GENUS.

General: The genus *Ceratium* was established by Schrank in 1793, the name being derived from the Greek for "small horn." The original description was somewhat inadequate: "Vermis inconspicuus amorphous rigidulus, corniculis circumferentiae pluribus." Schrank described two species, *C. pleuroceras* and *C. tetraceras*, which appear to belong to the polymorphic freshwater species, *C. hirundinella* (Müller) Bergh. As *Bursaria hirundinella* Müller (1773), this was the first species of *Ceratium* to be described. The first marine *Ceratium* to be described was *C. tripos* (Müller) Nitzsch (1817), as *Cercaria tripos* Müller (1776).

Several species of *Ceratium* were described during the period 1833–1873 as members of his genus *Peridinium* (1832), by the great microscopist Ehrenberg. Claparède & Lachmann (1858–1859) distinguished *Ceratium* from *Peridinium* on the basis of the horns. Stein (1883) was the first to realise that the composition of the thecal plates was the most satisfactory basis for the classification of the armoured Dinoflagellates, and accordingly differentiated between *Ceratium* and *Peridinium* (l.c.: 11), but did not establish the complete plate formula for *Ceratium*. Kofoid (1907b) showed the plate formula to be the same for all the ceratia he examined. He described the epitheca as having four precingular plates, but Jörgensen (1911) found the number to be five.

In the latter part of the nineteenth century, references to new species of *Ceratium* are either found in general works on Peridinians, sometimes not formally described, or in accounts of marine phytoplankton from different localities. The first work of this nature to deal with *Ceratium* extensively is Gourret's "Sur les Péridiniens du Golfe de Marseille" (1883).

The species concept in *Ceratium* was at first somewhat confused. Forms with distinctive shapes such as *C. gravidum* Gourret (1883) were recognised as distinct species; not so forms in which the antapical horns were directed anteriorly, or those with triangular epithecae and backwardly directed antapicals.

Some writers such as Bergh (1882) referred to the former as the "Formenkreis des *C. tripos*" and to the latter as the "Formenkreis des *C. furca.*"

Following Hensen's pioneer work on plankton (1887), the numbers of phytoplanktologists increased, stimulated by the realisation of the relationship between plankton and fishing and the organisation of oceanographic expeditions to all parts of the globe. The first large expedition, in the phytoplankton reports of which *Ceratium* is mentioned, was Hensen's Plankton Expedition of 1889 (Schütt 1892, 1895). A comprehensive series of illustrations of ceratia were published by Karsten (1905, 1907) in his account of the phytoplankton collected during the world-wide deep-sea Valdivia Expedition.

The first major monograph on *Ceratium* was that of Jörgensen (1911), which included detailed accounts of all the known species. This was followed by his work on the Mediterranean ceratia (1920), in which emphasis was placed on hydrological conditions and seasonal distribution, as Jörgensen wished to determine transportation of species from the Atlantic. A number of new taxa were included, sometimes without formal descriptions, and Jörgensen used the terms form and variety indiscriminately for the same taxon, occasionally giving new epithets to the typical infraspecific taxa of some species.

Many regional accounts of *Ceratium* followed, of which a few are mentioned below. Some dealt solely with the taxonomy of the species, others with the distribution of ceratia related to environmental conditions. Böhm (1931, Northern and Western Pacific) showed the range of variation in some species by a series of measurements and illustrations. Peters (1932, South Atlantic) and Steemann Nielsen (1934, South Pacific) considered the factors, in particular temperature, affecting both distribution and infraspecific variation. Peters considered distribution a criterion for the recognition of some problematic subspecific taxa. Steemann Nielsen included tables of measurements illustrating some aspects of infraspecific variation. Graham & Bronikowsky (1944, Pacific and North Atlantic) examined many hundreds of specimens and gave a comprehensive series of illustrations of infraspecific variation, with a most detailed account of distribution and associated hydrological factors, but unfortunately they included few measurements of specimens.

The next general taxonomic treatment of *Ceratium* was published by Schiller (1937) in Rabenhorst's Kryptogamenflora, and it is probably the basic reference for *Ceratium* most used by subsequent workers. There are, however, a number of errors in the bibliography and some of the subspecific categories are cited inaccurately.

Two postwar regional accounts of *Ceratium* are by Wood, in his studies of the Dinoflagellates of the Australian Region (1954, 1963), and Sournia (1967). Sournia's work on ceratia of the Mozambique Channel includes a useful comprehensive bibliography and a new unconventional approach to the treatment of some subspecific taxa. Sournia writes "... in the case of species which have a continuous sequence of morphological variations apparently related to temperature . . . to keep only to the name of the species . . . would . . . bury the problem . . . the usage of infraspecific taxa would . . . be multiplied by infinity." Pointing out that the genetic basis of variation is unknown, Sournia proposed that the rank "form" be applied to cases of variation not related to temperature, while infraspecific thermophylic and psychrophylic taxa should be classed as "varieties", with the cases with intermediate temperature preference given an epithet "outside the classical taxonomy", indicating the proximity to one or other of the varieties, e.g. "*C. horridum* (Cl.) Gran *horridum>buceros*."

Biometric methods of assessment of variation in taxa of *Ceratium* have been used by Lopez (1955, 1966) and Yarranton (1967). Lopez used measurements of antapical horn length and girdle diameter to analyse seasonal variations and relationships in members of the *C. tripos* complex and the Subgenus *Ceratium*. Yarranton showed that the determination of the coefficients of the curves of the three horns could be used as a basis of classification in the four taxa he studied.

The first major work on the cytology of *Ceratium* was that of Hall (1925) on mitosis in *C. hirundinella*, which includes a good account of earlier research. Later accounts are that of Skoczylas (1958) on mitosis in *C. cornutum* (Ehb.) Cl. & Lach., a general account of chromosome structure in the Dinophyceae by Dodge (1966) and the work of Jahn et al (1963) on the movement of ceratium flagella.

Cultural experiments on species of *Ceratium* have been carried out by Hasle and Nordli (1951) and Nordli (1957), and Nielsen (1956) has investigated factors causing variation in certain ceratia in their marine environment.

Chain formation, polymorphy and sexual reproduction: (See Fig. 1, G–L.)

The formations of chains of normal individuals of ceratia of similar size, with slight variation in disposition of antapical horns and apical horn length was recorded as early as 1830 by Michaelis, (*fide* Kofoid 1909). Kofoid noted that in a complete chain arising by normal vegetative division, the epitheca of the anterior member and the hypotheca of the posterior member are derived originally from the same cell.

Polymorphy in species of *Ceratium* was recognised by early writers such as Bergh (1882) and Hensen (1887), although their interpretation was incorrect. Hensen found small cells about one eighth to one tenth the size of normal *C. tripos* cells, with short backwardly or slightly laterally directed antapical horns. The former he considered were young forms of *C. furca* (Ehb.) Cl. & Lach, the latter young *C. tripos*. Lohmann (1908) was the first to discover typical *C. tripos* cells in chains together with similar sized or very slightly smaller heteromorphic cells, and in the same samples, a series of forms ranging from the small cells recorded by Hensen to normal *C. tripos* of normal size. He did not state specifically that he had found chains showing a continuous sequence from the very small heteromorphic cells to normal *C. tripos*, but wrote: "An dieser Ketten liess sich nun leich der Nachweiss führen, dass alle Jugendformen Hensens besondere Formen von *C. tripos balticum* sind . . ." He regarded these as "seasonal temporary variations" and suggested that the very small forms might conjugate.

Kofoid (1909), who found a chain of three heteromorphic *C. tripos* cells of similar size, suggested that Lohmann's small forms might be independent species unrelated to *C. tripos*. He considered the heteromorphic forms he found to be "mutants", arising due to environmental changes, in the course of asexual reproduction. Tschirn (1920, fide von Stosch 1964) illustrated a chain including a normal *C. tripos* and a heteromorphic form, smaller in size, due, it was suggested, to "depauperising division". Jörgensen (1920) encountered some single heteromorphic forms, similar to those found by Lohmann, which were "relatively frequent in the region (of the Mediterranean) of the fresher water from the Black Sea." He considered these to be "due to a degeneration, caused by certain hydrographical conditions," such as a variation in salinity.

In culture, a range of forms, not in chains, from small heteromorphic cells to normal *C. tripos* cells, was found by Hasle and Nordli (1951), and very small heteromorphic cells were found in a single cell culture of *C. horridum* (Cl.) Gran by von Stosch (1964). Von Stosch suggested that the end products of a differentiation series from a normal cell could not, by division, revert back to normal cells while the intermediates could.

Abnormal forms with extra horns were found both in culture and in nature by Hasle and Nordli.

The literature indicates that these heteromorphs and abnormally horned cells occur rarely in marine species, while very small heteromorphs have not been observed in freshwater species.

In the freshwater *C. hirundinella*, the number of antapical horns normally varies from one to three, sometimes up to five, (Kofoid 1907).

Sexual reproduction in a marine species: von Stosch (1964) observed a single instance of conjugation in a single cell culture of *C. horridum*, between a normal cell and a small heteromorph, the latter having been produced in the clone subsequent to its inception. The ventral areas of the two cells touched and the contents of the small cell rounded off and passed into the large cell. A later stage showed the plates of the presumed male gametophyte disintegrated in the region of the two nuclei which lay adjacent to one another. Von Stosch suggested that the thecal plates could have been "partially reabsorbed." Incipient fusion of the nuclei was observed but subsequent development is unknown.

Apstein (1910, fide von Stosch) reported a process of budding in *C. tripos*, where a small cell, similar to one of Lohmann's heteromorphs was observed budding off from the ventral area of a normal *C. tripos*. The later observations of von Stosch suggest that this could have been a misinterpretation of an instance of conjugation in *C. tripos*.

Encystment and sexual reproduction in freshwater species: Encystment in marine species has not been reported, but in freshwater ceratia encystment is known to occur, the cyst developing inside the theca of a normal shaped cell. A naked Gymnodinium-like swarmer, the Praeceratium stage, is liberated, which develops a theca (Schiller 1937). This divides into four daughter cells, which develop into normal adults, two of which inherit respectively the hypo- and epi- theca of the Praeceratium wall, (von Stosch 1965).

The actual division has not been observed, but von Stosch's observations (1964) on the configuration of the chromosomes of the Praeceratium nucleus, referred to as the "Knäuelstadium," indicate that it is a meiotic division. Following research on mitosis in *C. cornutum* by Skoczylas (1958) who found no stage resembling the "Knäuelstadium" during mitosis, von Stosch found that the chromosomes of the "Knäuelstadium" had the configuration typical of the post-zygotene stage of meiosis. According to von Stosch, a "Knäuelstadium" has been observed in certain marine ceratia of normal shape.

What was generally considered to be conjugation in *C. hirundinella* was first observed by Zederbauer (1904) and later by Entz (1924, fide Hall 1925), who described the joining together of two cells by a protoplasmic bridge. Actual nuclear migration was not observed, but the occurrence at the same time of numerous cysts was considered indicative that conjugation had taken place. Later Entz, (1930, fide von Stosch 1964), showed the apparent conjugation bridge to be an artefact. It is of interest to note that Paulsen (1909) observed specimens of the marine *C. lineatum* (Ehb.) Cl. with sacs with granular contents attached ventrally in the region of the flagellar pore, such as observed by Zederbauer in cells of *C. hirundinella* before "conjugation".

Von Stosch (1965) commenting on sexuality in *C. cornutum* wrote: "Der Sexualprozess, der direkt noch nicht beobachtet werden konnte, ist mit grösster Wahrscheinlichkeit heterogam." He observed in clones of *C. cornutum* the development of cells which differed from normal cells in size, being thinner, and in plastids and pigment content. These he termed "Mikroschwärmer." Later, binucleate cells were seen in the clone, with fragments of thecal plates on the ventral side, indicating that a process had occurred similar to the conjugation observed in *C. horridum*. These putative zygotes remained motile for a long time during which nuclear fusion took place. Later the protoplasmic cell contents rounded off, withdrawing from the horns, and a cyst membrane was formed within the thecal wall of the zygote.

Exuviation, Autotomy and regeneration: Kofoid (1908) observed specimens in which shedding or exuviation of certain thecal plates had occurred, and suggested that this could be an "adaptation to changed conditions of flotation". He also observed that many long horned ceratia had broken horns, and actually found cells with apparent abscission zones in the walls of as yet unbroken horns, and cells in which the theca surrounding the horn had broken off, leaving the protoplast surrounded by a uniformly thin layer, "impregnated with wall material?" extended horn-like beyond this. This was seen even in cells with almost the entire horn theca broken off. Kofoid concluded that regeneration of broken horns took place and that shedding of the horns was not necessarily accidental, and termed the active process of horn shedding autotomy. This he considered to be likewise a flotation adjustor.

Distribution and ecology: The work of Peters (1932) and Steemann Nielsen (1934) and Graham and Bronikowsky (1944) has been mentioned. Graham (1941) summarised his investigations of factors affecting the distribution of ceratia in the Pacific and North Atlantic with reference to the observations and conclusions of Peters and Steemann Nielsen. Graham found that variations in salinity did not appear to affect species distribution, while a geographic classification of the species could be made on the basis of temperature. Only three categories could be recognised, "cosmopolitan," "tropical" and "sub-polar," with no evidence of truly temperate species, the temperate latitudes being populated by tropical and cosmopolitan forms and occasionally sub-polar ceratia. Tropical species could be subdivided further according to the ranges of temperature at which they occurred, into "intolerant," with surface temperatures never less than 19°C, "slightly tolerant", "tolerant" and "very tolerant". Graham pointed out that currents could displace certain species from their "normal" temperature range. He further found that some ceratia increased in frequency from the surface to a depth of 100 meters, and, following Steemann Nielsen, classified them as "shade species".

SUBDIVISIONS OF THE GENUS

Vanhöffen (1896) divided *Ceratium* into four separate genera: *Ceratium* for species in which the antapical horns were directed forwards as in *C. tripos*; *Biceratium* for species in which the antapicals were not very dissimilar in length and directed backwards, as in *C. furca* (Ehb.) Clap. & Lach.; *Amphiceratium* for species with backwardly directed antapicals of very unequal length as in

C. fusus (Ehb.) Duj., and *Poroceratium* for species in which the epitheca was inflated laterally and lacked an apical horn, as in *C. gravidum* Gourret.

Gran (1902) treated the taxa *Amphiceratium* and *Biceratium* as Sections of the genus *Ceratium*, and proposed the name *Euceratium* for the Section containing species like *C. tripos*. As he was only dealing with plankton from Norwegian waters, he did not encounter members of the *Poroceratium* group.

Ostenfeld (1903) changed Gran's Sections to Subgenera and divided Subgenus *Euceratium* (Gran) Ostf. into two Sections: *Tripos* Ostf. and *Macroceros* Ostf., the former composed of species with the antapical horns closed at the distal end and horn lists without spines, the latter incorporating species with antapical horns open at the distal ends and spiny lists.

Karsten (1905, 1907) used his own classification. He placed all species with recurved or forwardly directed horns in "Subgenus *Ceratium tripos*" and used a trinomial system of nomenclature for these species e.g. "*C. tripos azoricum* Cl." Karsten (1907) divided this Subgenus into two Sections, *Protuberantia* in which the antapicals were initially backwardly directed and then recurved anteriorly and *Rotunda* in which the antapicals were forwardly directed from their inception. In part, these correspond to the Sections of Ostenfeld, but included in Section *Rotunda* was "*C. tripos platycorne*" (Daday) Karsten with spiny horn lists. Species belonging to the Subgenera *Amphiceratium* and *Biceratium* were treated as varieties of *C. furca*.

Kofoid's demonstration of the uniformity of thecal structure in species of *Ceratium* (1907b) supported the reincorporation of Vanhöffen's genera into a single genus. In 1909 Kofoid established the Subgenus *Poroceratium* (Vanhöffen) Kof. and divided Subgenus *Euceratium* (Gran) Ostf. into two Subgenera: *Tripoceratium* with rounded posterior margin and closed antapical horn tips, and *Macroceratium* with the characters of Section *Protuberantia* Karsten, and the tips of the antapical horns "truncate, open or contracted or rounded, but usually with terminal pore".

Jörgensen (1911) retained as Subgenera *Poroceratium*, *Biceratium*, *Amphiceratium* and *Euceratium*, dividing the last three into a number of Sections based upon horn and body characters: Subgenus *Biceratium*, Sections *Digitata* Jörg., *Lanceolata* Jörg., *Cornuta* Jörg., *Candelabra* Jörg. and *Furciformia* Jörg.; Subgenus *Amphiceratium*, Sections *Inflata* Jörg. and *Fusiformia* Jörg., and Subgenus *Euceratium*, Sections *Dens* Jörg., *Tripos* Ostf., *Limulus* Jörg., *Platycornia* Jörg., *Palmata* Jörg., *Macroceros* Ostf., and *Reflexa* Jörg.

In 1920, Jörgensen established a new Subgenus *Archaeceratium* incorporating Section *Digitata* Jörg. and Section *Poroceratium* (Vanhöffen) Jörg., and in Subgenus *Biceratium*, separated as Section *Pentagona* Jörg., *C. pentagonum* Gourret and its allies from Section *Furciformia*. Schiller (1937) followed this treatment, transferring Section *Lanceolata* Jörg. to Subgenus *Archaeceratium*.

Sournia (1967) also followed this classification, omitting Sections *Digitata* and *Lanceolata*, as he did not find the constituent species in his samples. As the type species of *Ceratium*, *C. hirundinella* (Müller) Bergh, was in the Subgenus *Biceratium* (Vanhöffen) Kof., Sournia replaced this name with Subgenus *Ceratium* (Article 22 of the International Code, Lanjouw 1966), and substituted Subgenus *Orthoceratium* Sournia for Subgenus *Euceratium* (Gran) Ostf., (Article 21).

Jörgensen (1920) distinguished Subgenus *Archaeceratium* from the other Subgenera on the nature of the apical plates of the epitheca. The nature of the apical plates has not, however, been recorded for all species of *Ceratium*.

These subdivisions of the genus are only applicable to the commonly occurring, so-called normal forms of *Ceratium*, for the backwardly directed horns of the small heteromorphic forms of *C. tripos* and *C. horridum*, members of the Subgenus *Orthoceratium*, are characteristic of the Subgenus *Ceratium*. Indeed, some authors have confused *C. lineatum* (Ehb.) Cl. belonging to this Subgenus with small heteromorphs of *C. tripos*, e.g. Paulsen (1908).

With the above reservations, Jörgensen's subdivision of *Ceratium* into Subgenera and Sections, with the alterations of Schiller and Sournia, is adopted in the following account.

CHARACTERS OF THE SUBGENERA

Subgenus **Poroceratium** (Vanhöffen) Kofoid.

The epitheca lacks an apical horn and apical plates four and two are greatly enlarged, composing most of the ventral and dorsal sides of the epitheca. Apical plates one and three are lateral, very narrow and boat-shaped. The antapical horns are posteriorly directed, only in *C. digitatum* Schütt, is the left antapical horn recurved anteriorly. The right antapical horn is never less than one quarter of the length of the left. All are marine species.

In the three remaining subgenera, in all the species examined, the four apical plates are of similar size, two on the ventral and two on the dorsal side of the epitheca, with apical plates one and four both in contact with the ventral area.

Subgenus **Ceratium.**

The apical horn is indistinctly to distinctly differentiated from the epitheca. The antapical horns are posteriorly directed, the right horn never less than one fifth of the length of the left horn. In freshwater species the antapicals vary in number from one to three, occasionally up to five. The only subgenus with both freshwater and marine species.

Subgenus **Amphiceratium** (Vanhöffen) Ostenfeld.

The apical horn is indistinctly to distinctly differentiated from the epitheca.

The cells, including the horns, are long and slender and the body is not very compressed. Both antapical horns are posteriorly directed, the right horn never exceeding one fifth of the length of the left horn, often it is much shorter, sometimes rudimentary or absent. Marine species.

Subgenus **Orthoceratium** Sournia.

The apical horn is distinctly differentiated from the epitheca. Both antapical horns are either anteriorly directed from their inception, or at first posteriorly directed and then recurved forward, except in *C. reflexum* Cl., where only the right horn is anteriorly directed. With two exceptions both horns are more or less similar in length. Marine species.

Subgenus **Poroceratium** (Vanhöffen) Kofoid (1909): 219.

Gen. *Poroceratium* Vanhöffen (1896): 133.

Subgen. *Archaeceratium* Jörgensen (1920): 6.

Diagnosis: Differs from the other subgenera in the nature of the apical plates. Apicals four and two are greatly enlarged composing respectively most of the ventral and dorsal sides of the epitheca, while apicals one and three are lateral, very narrow and boat-shaped.

The name is derived from the ring pore present in the epitheca of some of the species. Because the Subgenus had been enlarged to include species lacking a ring pore, Jörgensen (1920) changed its name to Archaeceratium.

According to Jörgensen (1911), the ring pore is a ring-shaped structure which is mounted on the inside of apical plates two and four, joining them tightly together, and allowing the protoplast no access to the inside of this ring. Kofoid (1907) described the pore as perforating the epitheca, which is not necessarily implied by Jörgensen. Kofoid also noted that the degree of development of the ring pore was subject to variation, "even to its suppression" in *C. gravidum* Gourret, the type species of Vanhöffen's genus. No later work seems to have been done on this structure. Graham & Bronikowsy's figures (1944) of *C. gravidum* include some specimens lacking a ring pore, while Wood (1963b) showed ring pores in figures of *C. praelongum* (Lemm.) Kof. and *C. digitatum* Schütt, both of which, according to other authors, lack a ring pore.

In *C. lanceolatum* Kof. and *C. gravidum*, the only apical plate to adjoin the ventral area is apical four, while in *C. praelongum* a small part of apical one also touches the ventral area. (See Fig. 2, D,E.) There is no indication in the literature of the relationship between the ventral area and the apical plates in the other species.

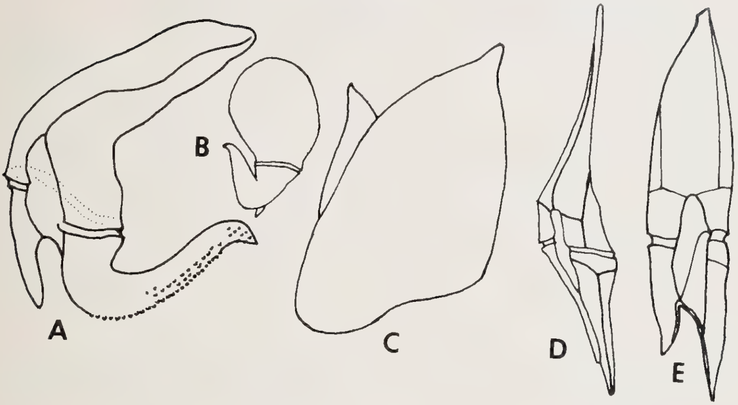

FIG. 2.

Fig. 2. *A* and *C*, (Schütt 1895), *C. digitatum: A*, latero-ventral view; *C*, ventral view of upper part of epitheca; *B*, (Peters 1932), "*C. digitatum var.*": dorsal view; *D*, (Graham & Bronikowsky 1944), *C. praelongum:* latero-ventral view; *E*, (after Kofoid 1907a), *C. lanceolatum:* ventral view.

Kofoid (1907b) numbered the large apical plates of this Subgenus as apical one, on the ventral side, and apical three, on the dorsal side, but Jörgensen (1911) considered them to be apicals four and two respectively. Jörgensen's numbering is adopted because in the other subgenera, both apicals four and one adjoin the ventral area, more or less equally, and in *C. praelongum*, the narrower of the two apicals adjoining the ventral area lies to the *left* of the much broader apical, and may be considered as apical one, with the inference that in *C. gravidum* and *C. lanceolatum*, apical one has been so displaced by the enlarged apical four that it no longer adjoins the ventral area.

KEY TO SECTIONS AND SPECIES.

I. Body slightly dorsiventrally compressed; epitheca dorsiventrally convex-concave or involuted forming longitudinal folds; left antapical horn markedly dorsally or dorsolaterally curved, spinulate.
Section *Digitata.*

II. Body markedly dorsiventrally compressed; epitheca flat and blade-like above ventral area; left horn never markedly curved as above, smooth.
  i. Epitheca in full dorsal or ventral aspect expanded laterally, apex rounded.
  Section *Poroceratium.*
  ii. Epitheca in full dorsal or ventral aspect lanceolate, apex a truncated point.
  Section *Lanceolata.*
  C. lanceolatum.

Section **Poroceratium.**

1) Lateral expansion of epitheca gradual, ring pore apparently always absent.
C. praelongum.

2) Lateral expansion of epitheca at base of apical plates fairly abrupt.
   A. Epitheca never broader than long, ring pore generally present. *C. gravidum.*
   B. Epitheca broader than long, ring pore always present. *C. cephalotum.*

Section **Digitata.**

1) Epitheca involuted to form longitudinal folds, tip of epitheca constricted to form a very short ill-defined apical horn, length of epitheca exceeding 190μ. *C. schroeteri.*
2) Epitheca dorsiventrally convex-concave, length of epitheca not exceeding 120μ. *C. digitatum.*
   A. Left antapical horn dorsally recurved so that its tip lies almost level with, to anterior to, girdle; apex of epitheca bluntly acuminate-cuspidate. *C. digitatum* subsp. *digitatum.*
   B. Left antapical horn dorsally recurved so that its tip lies some distance posterior to the girdle; apex of epitheca rounded. *C. digitatum* subsp. *rotundatum.*

Section **Poroceratium.**

Diagnosis: Differs from the other Sections in the rounded apex of the epitheca and in the marked dorsiventral compression of the body, particularly in the epitheca above the ventral area.

Jörgensen (1920) apparently intended to divide this Section into two Subsections, based upon the occurrence of the ring pore, but described only one Subsection, Annulifera, containing *C. gravidum* and presumably *C. cephalotum* (Lemm.) Jörg. The latter species and *C. praelongum*, which he considered transitional between Sections *Digitata* and *Poroceratium*, were absent from his Mediterranean samples. As the ring pore may be absent in *C. gravidum*, this subdivision seems inadvisable until the relationship between the apical plates and the ventral area is established in *C. cephalotum.*

Ceratium gravidum Gourret (1883): 58, pl. 1, fig. 15.
Schütt (1895) Pl. 11, fig. 41, 1–5; Vanhöffen (1896): 133; Okamura & Nishikawa (1904): 127, pl. 6, fig. 21; Kofoid (1907b): 182, figs. 7, 8; Jörgensen (1911): 10, pl. 1, fig. 8; (1920): 8; Forti (1921): 31, pl. 1, fig. 12, 13; Böhm (1931a): 351; Peters (1932): 28, pl. 2, fig. 12g; Steemann Nielsen (1934): 8, figs. 3, 4; (1939): 6; Schiller (1937): 357, fig. 389; Schubert (1937): 382; Graham & Bronikowsky (1944): 15, figs. 3 A–N, 4 P–U; Wood (1954): 272, fig. 186 a–c; Silva (1955): 155, pl. 7, fig. 1; Halim (1960) Pl. 4, fig. 21; Taylor* (1966): 463; Sournia (1967): 388, pl. 1, fig. 3.

Poroceratium gravidum Vanhöffen (1897): 382, pl. 5, fig. 12.
C. gravidum var. *angustum* Jörgensen (1911): 10, pl. 1, fig. 11.
C. gravidum var. *latum* Jörgensen (1911): 10, pl. 2, fig. 12; Forti (1921): 32, pl. 1, fig. 13.

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* Given in check-list.

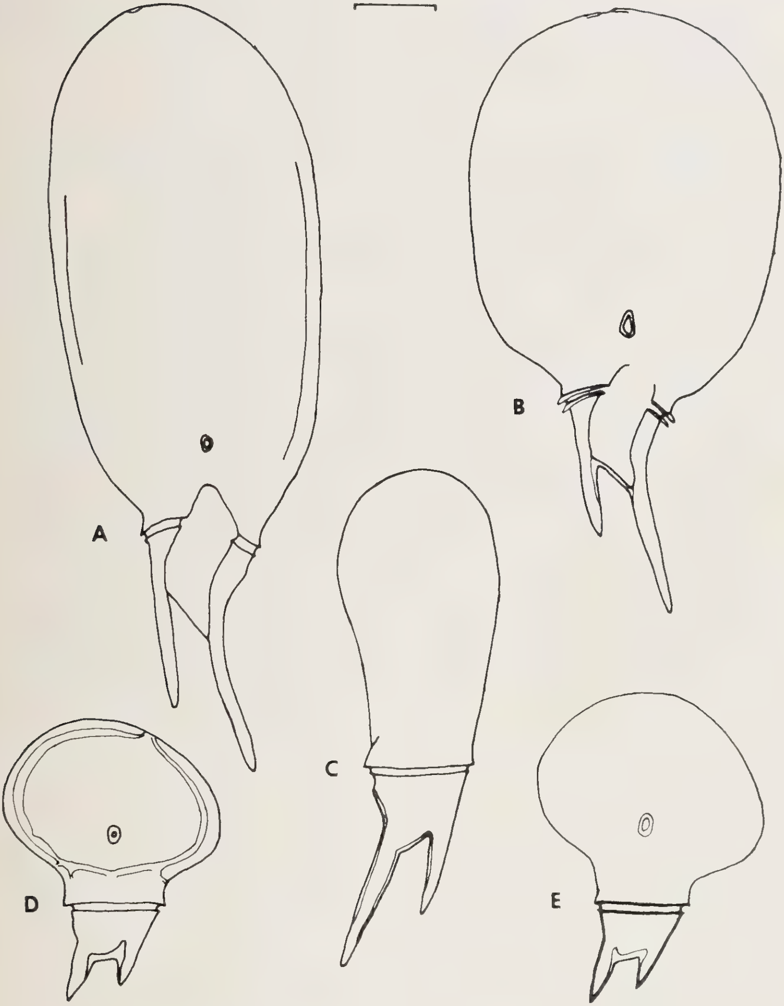

Fig. 3.

Fig. 3. *A* and *B*, *C. gravidum* in ventral view, apical pore and ring pore shown; in *B*, thecal wall shown in optical section at base of hypotheca and inner side of right antapical horn; *C*, *C. praelongum*, dorsal view; *D* and *E*, *C. cephalotum* in dorsal view; in *D*, sutures between epithecal plates partly discernible. Camera lucida drawings of specimens from stations in the Agulhas current. (The scale line indicates 50μ.)

C. gravidum var. *elegans* Jörgensen (1920): 10.
C. gravidum f. *obovatum* Jörgensen (1920): 8, fig. 4.
C. gravidum var. *elongata* Wood (1963b): 40, fig. 146.
C. oviformis Daday (1888): 102, pl. 3, figs. 7, 9.

Description: The mid body is dorsiventrally compressed, the compression becoming very pronounced above the ventral area, so that the part of the epitheca composed of the apical plates is flattened and blade-like. Seen in full ventral aspect, the *epitheca* is more or less obovate, the epithecal width varying from half to three quarters of the epithecal length; above the girdle, in the region of the precingular plates, there is only a slight increase in width relative to the girdle, then at the base of the apical plates the epitheca expands laterally fairly abruptly, less so in narrow forms, and sometimes slightly more on the right than on the left side; further lateral expansion is very gradual, maximum width being reached at half to two thirds of the length of the epitheca above the girdle; the apex is rounded, the apical pore displaced a little to the right; the ring pore, which may be absent, is situated medially in the lower half of the epitheca; the *hypotheca* tapers slightly to an oblique base. The *antapical horns* are parallel or slightly divergent, directed posteriorly or a little to the left, the left horn may be very slightly curved; the wall thickness and width of the horns varies and the right horn is generally half, sometimes three quarters of the length of the left. (See Fig. 3, A, B.)
Dimensions: In specimens examined: In full ventral aspect, girdle diameter 54–66μ; length epitheca 207–282μ; maximum width epitheca 144–198μ; length left horn 60–90μ; length left profile of hypotheca from base of horn to girdle about 42μ. *From literature:* Daday (1888), length epitheca 75–90μ; maximum width epitheca 70–75μ; length left horn from girdle 45μ; Jörgensen (1911), diameter 60–70μ; length epitheca 200–300μ.
Distribution: A widespread, but never abundant, shade species in tropical, subtropical and occasionally temperate waters. (See Table 1).

A subdivision of this species is unnecessary. Jörgensen's varieties were founded on variations in the shape of the epitheca due to differences in the width relative to the length. Peters (1932) considered these subdivisions superfluous on the grounds of their similar distribution. Graham and Bronikowsky (1944), after examining hundreds of specimens came to the conclusion that there was no discontinuity in the range of variation of forms, and gave a convincing series of illustrations, but no measurements.

Ceratium cephalotum (Lemmermann) Jörgensen (1911): 10, pl. 1, fig. 10.

Böhm (1931b): 43; Peters (1932): 28; Steemann Nielsen (1934): 7, fig. 2; (1939): 6; Schiller (1937): 356, fig. 388; Schubert (1937): 382; Graham &

Bronikowsky (1944): 15, figs. 2 A–C; Wood (1954): 271, fig. 185; Taylor* (1966) 462; Sournia (1967): 388, pl. 1, fig. 2; Nel* (1967): 98.

C. gravidum var. cephalotum Lemmerman (1900): 349, pl. 1, fig. 16; Karsten (1907): 415, pl. 50, fig. 1 a, b.

C. gravidum var. hydrocephala Schröder (1906): 369, fig. 44.

"Typenkreise der Gattung Ceratium" Schütt (1892): 269, fig. 79, 10a.

Description: The *epitheca* is dorsiventrally compressed and expanded laterally as in *C. gravidum;* seen in full ventral aspect, maximum epithecal width occurs at about mid epithecal length and is slightly more than, to one and a half times the epithecal length; the ring pore is apparently always present, approximately in the centre of the epitheca. The *antapical horns* are short and straight, the right horn about half the length of the left. (See Fig. 3, D, E.)

Dimensions: In specimens examined: In full ventral aspect, girdle diameter 45–48μ; length epitheca 111–114μ; maximum width epitheca 120–132μ; length left horn 27μ; length left profile of hypotheca from base of horn to girdle 27μ. *From literature:* Diameter 55μ; length epitheca 109–130μ; maximum width epitheca 157–170μ; length left horn 27μ.

Distribution: A rare species found in warm waters of all the oceans; not recorded from the Mediterranean. Graham and Bronikowsky describe it as a rare intolerant tropical shade species. (See Table 1).

There is some variation in the width of the epitheca, in particular with regard to the lateral expansion on the left side, but a subdivision of the species is superfluous. The variety described by Schröder is a specimen with a very broad epitheca.

Ceratium praelongum (Lemmermann) Kofoid ex Jörgensen (1911): 9, pl. 1, fig. 9; Kofoid (1907b): 182.

Paulsen (1930): 75, fig. 45; Böhm (1931b): 43, fig. 37a; Peters (1932): 28, pl. 2, fig. 12 f; Steemann Nielsen (1934): 7, fig. 1; (1939): 6; Schiller (1937); 356, fig. 387; Schubert (1937): 382; Graham & Bronikowsky (1944): 14, figs. 1 A–D; Silva (1957): 58, pl. 3, fig. 4; Wood (1963b): 40, fig. 148a, ?148b; Taylor* (1966): 463; Sournia (1967): 386, pl. 1, fig. 1.

C. gravidum var. praelongum Lemmermann (1900): 349, pl. 1, fig. 15; Ostenfeld & Schmidt (1901): 164; Karsten (1905b): 148; (1907): 415, pl. 50, fig. 2a, b.

The combination *Ceratium praelongum* was first used by Kofoid (1907) in a comment on the occurrence of the ring pore, which is apparently never present in this species. Wood's figure (1963, 148b) showing a specimen with a ring pore in the upper third of the epitheca is dubious.

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* Given in check-list.

Description: The *epitheca* is compressed as in *C. gravidum;* seen in full ventral aspect, there is a very gradual lateral expansion of the epitheca above the girdle, or, the sides of the lower half of the epitheca may be parallel, then enlarging very slightly; maximum epithecal width is reached two thirds of the epithecal length above the girdle and is half, sometimes up to two thirds of the epithecal length; there may be a slight concavity of the left profile in the region of the precingular plates, or at mid epithecal length, so that the epitheca appears to be slightly curved to the left; the apex is rounded to truncately rounded; a ring pore is apparently always lacking. (See Fig. 3,C.)

Dimensions: In specimen examined: In full ventral aspect, girdle diameter 57μ; length epitheca 162μ; maximum epithecal width 85μ; length left profile of hypotheca from base of horn to girdle 42μ; length left horn 57μ;. *From literature:* diameter 60–65μ (80μ according to Lemmermann); length epitheca 160–200μ; maximum epithecal width 85–100μ; length left horn 60–65μ (76μ according to Lemmermann).

Distribution: A fairly rare species occurring in warm waters of all the oceans and in the Mediterranean (Alboran Sea). Graham & Bronikowsky classify it as a rare, strictly tropical shade species. (See Table 1.)

Section **Digitata** Jörgensen (1911): 12.

Diagnosis: Differs from the other Sections in the slighter dorsiventral compression of the body, in the fact that the epitheca is dorsiventrally convex-concave or with longitudinal folds, and in the marked curvature of the left antapical horn which is spinulate.

Peters (1932), Steeman Nielsen (1934) and Graham and Bronikowsky (1944) placed the species of this Section in the Subgenus *Biceratium*. Jörgensen (1920) wrote: "As I now have found that *C. digitatum* possesses the same two broad ventral and dorsal apical and the very same characteristic boat-shaped lateral plates as *C. gravidum,* I propose to extend the subgenus Poroceratium to comprise *C. digitatum* (and *C. Schröderi*)." This is not a categorical statement that the epithecal plates of *C. schroeteri* are as in other members of this Subgenus and there are no further references to the matter in the literature. With this reserve, *C. schroeteri* is retained in Section *Digitata*.

Ceratium digitatum subsp. **digitatum** Schütt (1895) Pl. 12, fig. 42, 1–6.

Pavillard (1907): 230; (1916): 13; Jörgensen (1911): 12, pl. 2, fig. 13; (1920): 6, fig. 1; Forti (1921): 32, pl. 1, fig. 14; Böhm (1931a): 350; Peters (1932): 28;

TABLE 1. Showing distribution and relative frequency, expressed as a percentage, of species of the Subgenus *Poroceratium* in samples from the line of NGY stations off Port Elizabeth. Apart from the * stations, net hauls examined from 100–0m. (Temperatures in °C.)

	MARCH							MAY							
NGY Stations.	**11***	**12**	**13**	**14**	**15**	**16**		**41***	**42**	**43**	**44**	**45**	**46**		*Spot records from other stations.*
Surface temperature	20·66	24·28	25·49	23·78	22·19	21·62		17·49	23·27	24·15	23·50	21·25	20·90		
Temperature at 100m	13·26 (at 50m)	17·53	19·65	19·52	18·73	18·61		16·66 (at 50m)	12·21	19·99	20·54	20·50	20·37		
No. slides examined	4	4	4	4	4	8		4	5	7	4	4	5		
Total number ceratia	601	191	233	267	270	241	1803	318	92	197	184	241	365	1397	
C. GRAVIDUM	—	0·52%	0·43%	—	—	—	0·11%	—	—	—	—	1·24%	0·27%	0·29%	
C. CEPHALOTUM	—	—	0·86%	—	—	—	0·11%	—	1·09%	—	—	0·41%	—	0·14%	
C. PRAELONGUM	—	—	—	—	—	—	0·00%	—	—	—	—	—	—	0·00%	NGY 30
C. DIGITATUM SSP. DIGITATUM	—	—	—	—	—	—	0·00%	—	—	—	—	—	—	0·00%	NGY 76
C. DIGITATUM SSP. ROTUNDATUM	—	—	—	—	—	—	0·00%	—	—	—	—	0·41%	—	0·07%	
C. SCHROETERI	—	—	—	—	—	—	0·00%	—	—	—	—	—	—	0·00%	NGY 30

Steemann Nielsen (1934): 8, fig. 5; (1939): 6; Schiller (1937): 358, fig. 392; Schubert (1937): 383; Rampi (1939): 302, fig. 3; Graham & Bronikowsky (1944): 16, figs. 5, C–E; Gaarder (1954): 11; Taylor* (1966): 463;? Wood (1963b): 39, fig. 144.

"Typenkreise der Gattung Ceratium" Schütt (1892): 269, fig. 79, 11.
?"*C. digitatum var.*" Peters (1932): 28, pl. 4, fig. 19.

Description: The body is slightly dorsiventrally compressed in the region of the girdle, ventrally concave, dorsally convex; in the *epitheca*, the dorsiventral convex-concave curvature becomes more marked; about one third of the epithecal length above the girdle, the epitheca curves dorsally and slightly to the left at an angle of about 45° to almost 90°; the apical third is flatter, slightly more compressed, with the sides, until now almost parallel, tapering to a bluntly acuminate cuspidate apex, set somewhat to the left, in the blunt point of which is the apical pore. The *antapical horns* are dissimilar, the right relatively short and straight, the left much stouter, directed posteriorly for a very short distance, then curved dorsally to slightly dorsolaterally, through an angle of about 135°, so that the tip, which is recurved, lies almost level with, to anterior to, the girdle; the left horn is spinulate, with the thecal wall on the inside of the curve thickened along the suture between the antapical plates. (See Fig. 2, A, C; Fig. 4, D).

Dimensions: In single damaged specimen found: Girdle diameter in full dorsal aspect, 42μ; length epitheca, approximately 120μ; length recurved part of left horn, 75μ. *From literature:* Jörgensen (1911), girdle diameter in full vextral aspect, 50μ or more, seen sideways, 40–45μ; length epitheca 90μ; length right horn, 25μ.

Distribution: Rare warm water taxon, recorded from all the oceans and the Mediterranean. Graham and Bronikowsky classify it as a rare, intolerant tropical shade species. (See Table 1.)

The single damaged specimen found in the present survey was seen only from the dorsal side. The antapical horns were similar to those of Schütt's iconotype, but the typical blunt acuminate point of the epithecal apex was not apparent, possibly due to the position of the specimen. The left side of the epithecal apex was not rounded but bluntly angled.

Peters found and illustrated a specimen "*C. digitatum var.*", "die einen noch breiteren Vorderkörper besizt, als die von Jörgensen beschreibene breite *f. rotundatum*". No other description is given. In the figure, the antapical horns resemble those of Schütt's iconotype, but the epithecal apex is rounded. This could be due to the angle at which the specimen was drawn. If however the apex was indeed rounded, then the specimen differs sufficiently from Schütt's iconotype to be considered as a separate taxon. (See Fig. 2, B.)

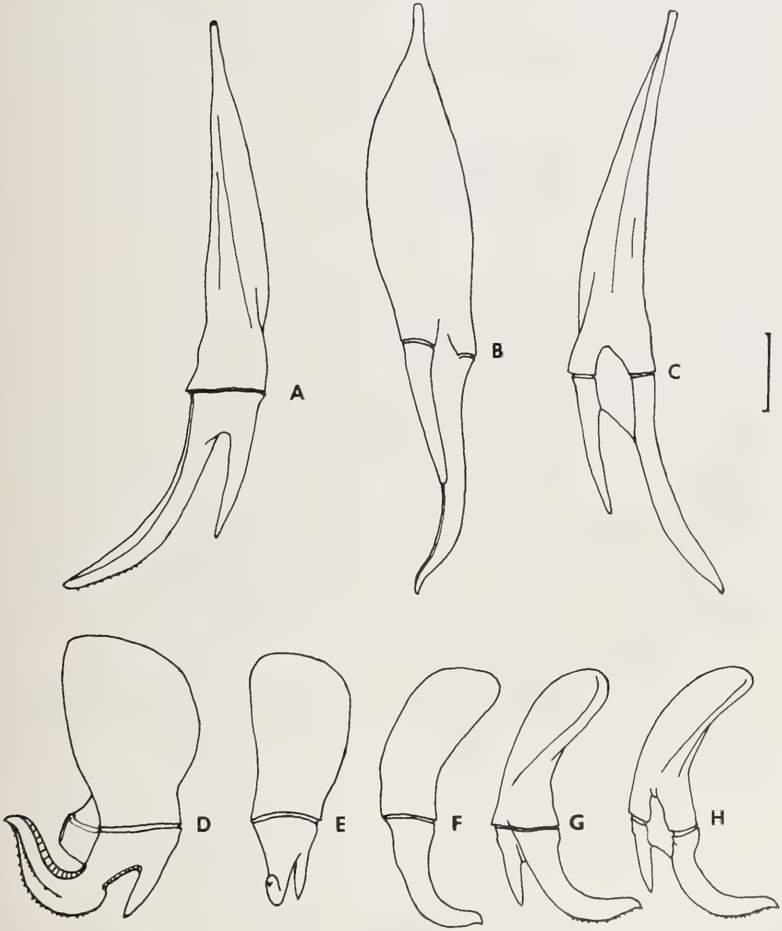

FIG. 4.

Fig. 4. *A*, *B* and *C*, *C. schroeteri*: *A*, dorsal aspect, thickening of thecal wall along outer side of left antapical horn shown in optical section; *B*, latero-ventral aspect; *C*, ventral aspect; *D*, broken specimen of *C. digitatum* subsp. *digitatum* ? dorsal view; *E*, *F*, *G* and *H*, *C. digitatum* subsp. *rotundatum* in dorsal, lateral, latero-ventral and ventral view. Camera lucida drawings of specimens from stations in the Agulhas current. (The scale line indicates 50μ.)

Graham & Bronikowsky noted little variation, except in the length of the left horn, in specimens of subsp. *digitatum* from the 26 stations at which it was found in the Carnegie samples.

Wood's inclusion of a ring pore in the upper third of the epitheca in a figure of subsp. *digitatum* is questioned. There is no mention in the literature of a ring pore in the species.

Ceratium digitatum subsp. **rotundatum** (Jörgensen) Reinecke stat. nov.

C. digitatum var. rotundatum Jörgensen (1920): 7, fig. 2a, b; Böhm (1931a): 350; Graham & Bronikowsky (1944): 16, fig. 5, A, B; Gaarder (1954): 11, fig. 12.

Diagnosis: Differs from the type in the less marked dorsal curvature of the left antapical horn, the tip of which lies some distance posterior to the girdle, and in the rounded apex of the epitheca.

Description: The *epitheca* is compressed, dorsiventrally convex-concave and curved as in the type, except that the curvature is more lateral; the epithecal apex is rounded, with the apical pore laterally placed. The *left antapical horn* which is spinulate, with the wall thickened as in the type, curves gradually laterodorsally, at an angle not exceeding 90° so that the tip, which is recurved, lies some distance posterior to the girdle. (See Fig. 4, E–H.)

Dimensions: In specimen examined: Semi-lateral girdle diameter, 42μ; approximate length epitheca, 120μ; distance from left side of girdle to tip of left horn, 96μ. *From literature:* Jörgensen (1920), girdle diameter, 59μ; Gaarder (1954), diameter 42μ; length 175μ.

Distribution: Extremely rare. Recorded from the Mediterranean (Jörgensen 1920, Böhm 1931a), South of the Azores (Gaarder 1954), in the Guinea Current (Jörgensen 1920), South of Easter Island (Graham & Bronikowsky 1944) and in the Agulhas Current. (See Table 1.)

The differences between this taxon and the type are sufficiently great to justify a taxonomic status exceeding that of variety. Examination of more specimens may warrant its treatment as a separate species. Graham and Bronikowsky found no intergrades between subsp. *digitatum* and the two specimens of subsp. *rotundatum* found in the Carnegie samples.

Ceratium schroeteri Schröder (1906): 368, fig. 43.

Kofoid (1907): 173, pl. 3, figs. 18, 19; Jörgensen (1911): 12, pl. 2, fig. 14; (1920): 8, fig. 3; Böhm (1931a): 350; Pavillard (1931): 67, pl. 2, fig. 15; Schiller (1937): 358, fig. 391; Silva (1956): 67, pl. 12, figs. 1–3; Wood (1963b): 42, fig. 150; Taylor* (1966): 463.

Description: The body is slightly dorsiventrally compressed in the region of the girdle; the *epitheca* in full ventral aspect is narrowly conical, tapering gradually towards the tip, very slightly inclined laterally to the left; on the right, the epitheca is expanded dorsolaterally into a longitudinal fold or hollow keel visible from the front, which rises a short distance above the girdle; a similar fold, not as sharply defined, arises on the ventral side above the ventral area; both expand gradually, then narrow a short distance behind the epithecal tip giving the epitheca in semilateral aspect a lanceolate profile with a short ill-defined apical horn; a third poorly defined fold is found on the dorsal side. The *antapical horns* are dissimilar, the right about half the length of the left straight or slightly curved to the left; the left horn is spinulate, dorsolaterally curved in a gradual arc; the tip may be recurved; the thecal wall of the left horn is thickened at the suture between the antapical plates along the inside of the curve. (Schroder illustrates a similar thickening along the edge of the right fold of the epitheca, not seen in the Agulhas specimen.) See Fig. 4 A–C.)
Dimensions: In single specimen found: Semi-lateral diameter, 42μ; length epitheca, 222μ; distance from tip of left horn to girdle, 130μ; the same for the right horn, 72μ; *From literature:* Total length, 335–342μ; diameter, 47–50μ; length epitheca, 203–212μ.
Distribution: Extremely rare warm water species recorded from all the oceans and the Mediterranean. (See Table 1.)

Section **Lanceolata** Jörgensen (1911): 13.

Diagnosis: Differs from the other Sections in the dorsiventral compression of the body together with the lanceolate shape of the epitheca, as seen in full ventral aspect, and in the nature of the epithecal apex which is a truncated point.

Ceratium lanceolatum Kofoid (1907): 172, pl. 3, fig. 17.

Jörgensen (1911): 13, pl. 2, fig. 15; Schiller (1937): 358, fig. 390; Gaarder (1954): 13, fig. 13.

?"Typenkreise der Gattung Ceratium" Schutt (1892): 269, fig. 79, 10b.

Description: The *epitheca* is dorsiventrally very compressed above the ventral area; in full ventral aspect it is lanceolate, with the apex a truncated point. The antapical horns are directed posteriorly, the right about the half length of the left. Ring pore apparently absent. (See Fig. 2 E.)
Dimensions: From the literature: Kofoid (1907), diameter, 19–22μ; length 95–122μ; Gaarder (1954), diameter, 56μ; length 285μ.
Distribution: Apparently only recorded twice, West of Peru (Kofoid 1907) and West of the Azores (Gaarder 1954), (and possibly the record of Schütt 1892).

The figure given by Schütt illustrates a specimen approximating the dimensions given by Gaarder. A teardrop shaped structure is shown in the middle of the epitheca, which, when compared with the illustration of the ring pore in the adjacent figure of *C. cephalotum*, appears to represent a ring pore.

DISTRIBUTION OF THE SUBGENUS POROCERATIUM IN THE AREA STUDIED.

During International Geophysical Year 1958, 76 N50V net samples were taken at 100–0m and 50–0m, from stations in the Agulhas current along offshore lines between Durban and Plettenberg Bay, during three cruises in February and March, May and August of 1958.

An assessment of the relative frequency of the diatoms and armoured dinoflagellates was made by examining diluted drops of the samples and recording the first 300 to 600 diatom cells, (depending upon density), and the armoured dinoflagellates encountered during the process. A total of 30,323 diatom cells and 974 armoured dinoflagellates, of which 417 were ceratia, was counted. The numbers of armoured dinoflagellates recorded in this way ranged from 0 per 600 diatom cells to 125 per 310 diatoms. The percentages of ceratia relative to the total number of diatoms and armoured dinoflagellates, and to the number of dinoflagellates alone, were 1·33% and 42·61% respectively.

Samples collected during the March and May cruises from a line of 6 stations off Port Elizabeth, were examined in more detail for their ceratium flora.

The relative rarity of the species of the Subgenus *Poroceratium* in this area is indicated by their absence from the general diatom-armoured dinoflagellate count, and their low percentage frequency in the detailed examination of the Port Elizabeth line samples. (See Table 1.)

ACKNOWLEDGEMENTS

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